FROM FLOOD AVOIDANCE TO FORAGING: ADAPTIVE SHIFTS IN TRAPDOOR SPIDER BEHAVIOUR

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Fossorial habits protect many mygalomorph spiders from both biotic and environmental factors. However burrows in some habitats are vulnerable to sheet flooding. Spiders in diverse habitats counter the hazard of flooding in various ways. A comparative account of adaptive specialisations, particularly of burrows, in flood avoidance is presented. Such primary modifications sometimes lead to new foraging opportunities. Examples are given of modified foraging as a consequence of burrow adaptations. The origins of such constructions are hypothesised in relation to changing climatic regimes and modified habitats. The idiopid genera *Homogona* Rainbow and *Neohomogona* Main are restored from synonymy.

☐*Mygalomorphae, Trapdoor spiders, burrows, flood avoidance, foraging, Australia.*

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Most mygalomorph spiders are terrestrial and either make burrows, silk tubes or webs or combine a web with a burrow. A few are arboreal and either make tubes in the bark of trees or have webs in crevices or under bark; their nests are generally not associated with foliage. Of the 15 currently recognised families of Mygalomorphae (Raven, 1985), 10 occur in Australia and of these, seven have at least some representatives with trapdoors. A burrow provides protection from the physical environment, from weather conditions and from predators and parasites; it provides a brood chamber for eggs and spiderlings. A burrow is also a lair from which a spider perceives and ambushes or intercepts prey; thus it provides a foraging base. All these functions have been commented on many times in the literature over the last century, the earliest comprehensive study possibly being that of Moggridge (1873, 1874).

In its simplest form a burrow has an 'open' entrance from which a spider makes short sorties in pursuit of prey. In extreme habitats, the entrance may be sealed with silk or soil for added protection during certain times of the year, for example during summer drought or winter snow falls. Folding collars and finally hinged doors give maximum security and protection. The protective advantage of a door has been shown to be offset by the hinge-line inhibiting the foraging area of a spider but nevertheless many door builders have overcome this disadvantage by various modifications to the burrow (Coyle, 1981; Main, 1986).

This paper discusses the adaptive behavioural responses associated with nest structure and site, of Australian mygalomorph spiders, to the hazard of flooding and shows that these primary adaptations have sometimes secondarily created new foraging opportunities for spiders. In particular the previously unreported nest of an undescribed species of *Aname* which exhibits both 'primary' and 'secondary' responses in its flood-avoidance tactics is described also.

FLOOD AVOIDANCE BEHAVIOUR

In certain terrestrial habitats, burrows and silk tubes and webs face the physical hazard of flooding. Generally the complexity of habitats in rainforest and mesophyll forest provides some sort of buffer against flooding; there is greater capacity for absorption of rainfall in the vegetation and litter of a forest floor than there is for example in desert or semi-arid country where sheet flooding on bare ground is a common phenomenon. Even so some rainforest situations are subject to water logging and flooding associated with torrential downpours. Likewise where rain is markedly seasonal as in monsoon rainforests the alternation of wet and dry conditions means that some habitats experience sudden saturation or inundation. Main (1976, 1982b) and Cloudsley-Thompson (1982, 1983) discussed some of the burrow modifications of mygalomorphs which prevent flooding. Avoidance of flooding is different to behaviours whereby spiders withstand immersion by enclosing the body in a bubble of air.

In summary, in avoiding flooding of nest sites, mygalomorph spiders have adapted behaviourally in several ways:

(1) By moving the nest site–behaviour prior to, during or after the event.

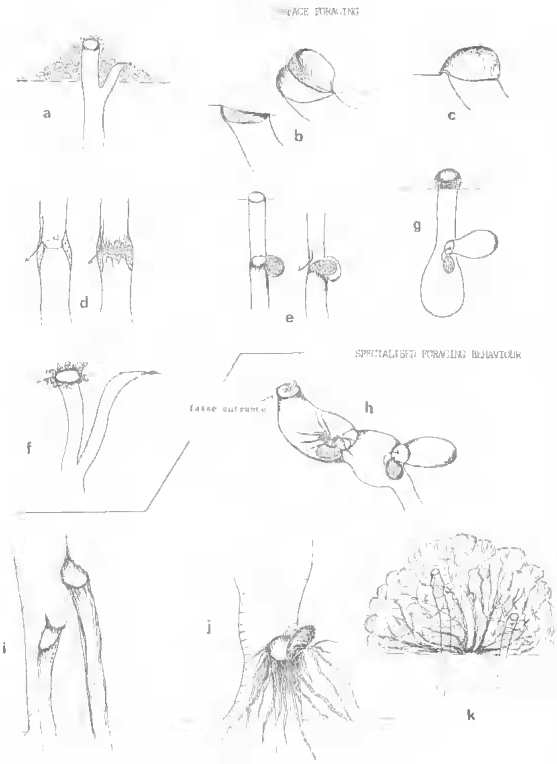

FIG. 1. Flood avoidance specialisations of mygalomorph burrows: (a) soil and pebble levee of *Kwonkan wonganensis*; (b) bath plug door (Idiopidae); (c) dome or 'cap' of an *Aganippe* species (Idiopidae); (d) 'sock' of *Anidiops* (Idiopidae); (e) 'pebble' and collar closure of burrow of *Stanwellia nebulosa* (Nemesiidae); (f) side shaft and escape 'hatch' of burrow of *Aname diversicolor* (Nemesiidae); (g) side shaft with door in nest of *Idiommata* sp. (Barychelidae); (h) profile of nest of a *Teyl* sp. (Nemesiidae) with entrance atrium and subterranean doors (and sideshaft); (i) aerial tube of *Misgolas robertsi* (Idiopidae) supported on tree trunk; (j) extended tube with trapdoor of *Aganippe castellum* (Idiopidae) supported against stem of shrub; (k) silk and soil tube of 'turret-building' *Aname* sp. (Nemesiidae) in foliage of shrub.

(2) By permanently reinforcing the nest e.g. burrow (and/or opening) against inundation–prevention.

(3) By modifying the nest structure so that part of it is safeguarded against inundation–prevention.

(4) By modifying the nest so that it is (in part) sited beyond the reach of intermittent flooding–prevention.

(5) By adopting an arboreal instead of terrestrial habitat.

Examples of these adaptations will now be given.

(1) Mygalomorphs elsewhere have been recorded as moving nest sites prior to inundation. The Amazonian web-weaving diplurid *Ischnothele guianensis* makes webs on tree trunks in the rainforest which is seasonally inundated. Spiders move their web sites higher up the trunks as the water level rises (Hofer, 1991). The Australian diplurid genus *Cethegus* (curtain web spiders), which makes copious webs sometimes associated with a burrow retreat, amongst stones, or against logs or shrub stems, is widespread across tropical Australia, the interior and southwestern Western Australia (Main, 1960, 1991a and unpublished; Raven, 1984). A study on a species at Durokoppin in the Western Australian wheatbelt showed that the spiders move their web sites after rain damage (Main, unpublished). Another species which occurs amongst the rocks of water courses in the Kimberley rainforest patches (Main, 1991a) presumably moves web sites during the 'wet' when the habitat is inundated. Although dependent on a web for prey capture these spiders are remarkably agile on the ground, and thus could readily decamp if flooded out of their nest sites, following which a web could be readily reconstructed (unlike some architecturally complex burrows of other mygalomorph families).

(2) Even 'open' burrows, if lined with silk frequently have collapsible or folding collars which can prevent flooding, for example as in many nemesiids and some *Misgolas* species, e.g. *M. pulchellus* (Rainbow & Pulleine) (pers. obs.). Collars are sometimes strengthened with litter or by a surrounding pile of soil or silk-bound pebbles (Fig. 1a) e.g. the levees of some nemesiids including *Kwonkan wonganensis* (Main) (originally described as *Dekana* (Main, 1977, plate 15)) (see also Main (1981, plate 1, fig. d) with reference to the levee of a 'diplurine' burrow). The ctenizid *Conothele*, the actinopodid *Missulena* and some barychelids have secure doors and parchment or canvas-like, silk linings which are more-or-less impermeable. Most idiopid species construct well defined burrows and all except some species of *Homogona*[1], *Neohomogona*[1] and *Misgolas* have a trapdoor. Many idiopid species which have adapted to flood-prone habitats, ranging from rainforest to desert

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[1] The idiopid genera *Homogona* Rainbow and *Neohomogona* Main were synonymised with *Cataxia* Rainbow by Raven (1985). They are here formally restored from synonymy and diagnosed in Main (1985).

and particularly in bare ground or sloping creek banks, frequently have permanently reinforced burrows including thick plaster walls coated with dense silk, and thick, close fitting bath-plug like doors or tightly fitting caps (Figs 1b, c). Such secure nests also provide protection against predators, parasites and adverse physical conditions, including dessication.

(3) Some species of Idiopidae, Nemesiidae, Barychelidae and Hexathelidae safeguard particular areas of their burrows against inundation. Such safeguards include (a) special blocks in the lumen or (b) sideshafts with 'escape' hatches or (c) one or more sidechambers with 'internal' trapdoors. Examples of the above are:

(a) Some species which have either an open entrance (e.g., *Misgolas* spp.) or a flimsy door (e.g., *Anidiops*) have a collapsible collar ('sock', see Main, 1957, 1976, plate 9 and 1985, figs 209, 210) consisting of a detachable section of the silk lining which can be pulled downwards by the spider thus blocking the burrow (Fig. 1d). Water seeping down the walls or flowing into the burrow is deflected by the infolded 'neck' of the sock and soaks into the surrounding soil leaving the lower section of the silk lined burrow unflooded. A similar structure in *Stanwellia nebulosa* (Rainbow & Pulleine) (Fig. 1e) is further reinforced by an attached, artificial pebble which seals the lower silk lined part of the burrow (Rainbow & Pulleine, 1918, pl. 20; Main, 1964, 1972 figs 22a, b, 1976). Although these devices are generally considered a protection against predators (see Main, 1956a regarding *Anidiops* (=*Gaius*) their original function was probably prevention against flooding (see Main, 1976 regarding *Stanwellia*).

(b) Nests of some species have silk sideshafts with 'escape' hatches at the surface (see Fig. 1f) which probably enable the spiders to escape flooding as well as intrusive predators. Examples are the burrows of 'wishbone' spiders of the genus *Aname* (Main, 1982a, fig. 1; 1976, pl. 10) and *Misgolas ornata* (Rainbow) (Main, 1985: 33).

(c) Sideshafts with 'internal' trapdoors are constructed by several undescribed species of *Teyl* (Nemesiidae) (earlier attributed to *Ixamatus*, see Main (1976, pp. 86-88, fig. 21)), by *Hadronyche* (Hexathelidae) (see Main, 1964:40, fig. j; 1976, fig. 18c; Gray, 1984, fig. 31 (described as *Atrax*)), *Idiommata* (Barychelidae) (Main, 1976, fig. 19d; Raven & Churchill, 1991: 35) and *Missulena* (Actinopodidae) (Main, 1956b). While the sideshafts of all species studied are known to function as brood chambers and also sometimes as protection from predators it is probable that the original function was that they offset flooding of the main shaft of the burrow (see Fig. 1g). Considering the habitat of *Teyl* species this is unequivocal.

(4) Burrows of some species are continued as tubes above the ground or litter surface and may be strengthened into free standing palisades (by the attachment of leaves, twigs and debris) which deflect sheet flooding in bare ground or prevent immersion in water-soaked litter. Examples include the tubes of *Homogona cunicularius* Main (Main, 1983, fig. 15), *Misgolas hirsutus* (Rainbow & Pulleine) (pers. obs.) and *Neohomogona stirlingi* and *N. bolganupensis* Main (Main, 1985, fig. 219). Tubes that extend a considerable distance above the substrate are attached to rocks, tree buttresses, exposed roots e.g. *Misgolas robertsi* (Main and Mascord) and related species (Main and Mascord, 1974, pl. 1a, b; Mascord, 1970 pl. 2 fig. 4), logs e.g. *Cataxia maculata* Rainbow (Main, 1969, figs 30, 31) or stems of shrubs e.g. *Aganippe castellum* Main (Main, 1986, figs 2, 4i; 1987, fig. 6). The first examples have open tubes, sometimes with flanged, collapsible collars but *A. castellum* has a trapdoor (Figs 1i, j). All are effective in flood avoidance by having the entrance above the 'flood level' following a deluge.

The previously undescribed but remarkable burrow/tube of an undescribed species of *Aname* extends as a turret-like tube amongst supporting foliage of shrubs. The genus *Aname* which is widespread but endemic in Australia and Tasmania, occurs in varied habitats, is taxonomically diverse and includes many undescribed species.

The turret-building species occurs in semi-arid country in southeastern Western Australia and Eyre Peninsula in South Australia. Nests have been observed in mallee/spinifex associations (*Eucalyptus*/*Triodia*) (Figs 2a, b, c) but also in mulga and amongst chenopod shrubs in seasonally swampy habitats. The spiders make shallow burrows lined with silk which extend as tubes into the foliage of supporting tussocks or shrubs and open either within the foliage or above the canopy (Fig. 1k). The outside of the tube is heavily but irregularly coated with soil. During and after rain, sheet flooding occurs in such sites, and particularly in the sandy loam of mallee/spinifex associations, water flows in a slurry around the spinifex hummocks. Burrows appear to be deepened (and/or remade) after rain and the sodden spoil dumped on the lip of the tube and outside the

Siting of burrow opening		PRIMARY ADAPTATION		SECONDARY ADAPTATION
		Flood avoidance through modified burrow structures	Unmodified foraging	Specialised foraging in response to 'new' opportunities
FOSSORIAL	Ground	—open* burrows: collars& folding collars & levees	surface	
		—closed* burrows: reinforced walls & doors	surface	
	Subterranean	— sub-surcae closures of lumen (open or closed burrow)	surface	
		—supernumerary chambers with doors		subsurface (pitfall captures)
	Elevated	extension of open tubes against vertical support		arboreal and semi-aerial
		—extension of closed burrow (with door) against plant stem		arboreal
		extension of open tube into foliage		foliage canopy
CORTICOLOUS		— open or closed tubes in bark		arboreal

TABLE 1. Siting of mygalomorph burrows primarily modified in flood avoidance and those secondarily resulting in specialised foraging methods. * open = without door; closed = with trapdoor.

entrance. Thus the turret is heightened progressively while much of the paste-like spoil pours down the outside wall, solidifying into a kind of stucco as it does so. Tubes up to 25cm have been observed within the supporting scaffolding of spinifex hummocks. The sometimes bulky structures belie the relatively small size of the artificers (up to 4.5mm carapace length). Occasionally free-standing tubes (but small and only up to 10cm high), away from shrubs, are found (see Main, 1982b, fig. 2). Most unsupported tubes may collapse (at ground level) and be destroyed during flooding while at least the aerial section of those amongst the tussocks remain relatively intact.

(5) Mygalomorphs which have their nests sited completely on the trunks of trees are found only in very wet forests. Their nests in such situations appear well protected against inundation. Australian examples include theraphosids which make silk retreats under bark in north Queensland (pers. observation), the nemesiid, *Chenistonia villosa* Rainbow and Pulleine which makes defined silk tubes in crevices of *Casuarina* bark in the karri forest of southwest Western Australia (pers. observation), species of the ctenizid, *Conothele*, in tropical Queensland (Main, 1976) illustrated in McKeown (1963), the barychelid *Sason* in north Queensland (Raven, 1986) and migids e.g. *Moggridgea tingle* Main (Main, 1991b). *C. villosa* and *M. tingle* both make nests in the ground also, in sites not vulnerable to water logging. This is probably a secondary habitat adopted in response to gradual drying of the climate and environment where the bark of trees would be subject to dessication.

NEW FORAGING OPPORTUNITIES

Foraging 'techniques' of mygalomorphs are closely associated with burrow structure. Burrows of some species are constructed with special adjuncts that enhance foraging, such as silk trip threads or attached twiglines. Main (1957, 1982b, 1987) described some combinations of burrow structure, morphology and foraging behaviour in relation to the habitats occupied and noted the relative efficiency of the various foraging strategies.

In modifying behaviour and burrow structure in flood avoidance, some species have as a consequence been exposed to 'new' foraging opportunities. Table 1 summarises the categories of 'primary' burrow modifications and sitings associated with flood avoidance and any 'secondary' changes of foraging behaviour. Reinforcement to burrows and doors which do not involve alteration of siting of the entrance, do not generally result in modification of foraging method. However, any modifications which alter the siting of burrow entrances away from the surface of the ground do result in specialised (predatory) foraging behaviour.

A striking example of a subterranean entrance is that constructed by a group of *Teyl* species. Although most species of *Teyl* have open burrows, a few build doors in flood avoidance. Several species have surface doors in bare open ground but the foraging method is similar to that of species with open holes (Main, 1986). Several species which occur in deep litter in seasonally flood-prone, braided creeks and the flats around salt lakes in southern Western Australia have evolved a further specialisation. An open 'false entrance' leads into a cup-like pouch or atrium which has on its inner wall a trapdoor (entrance

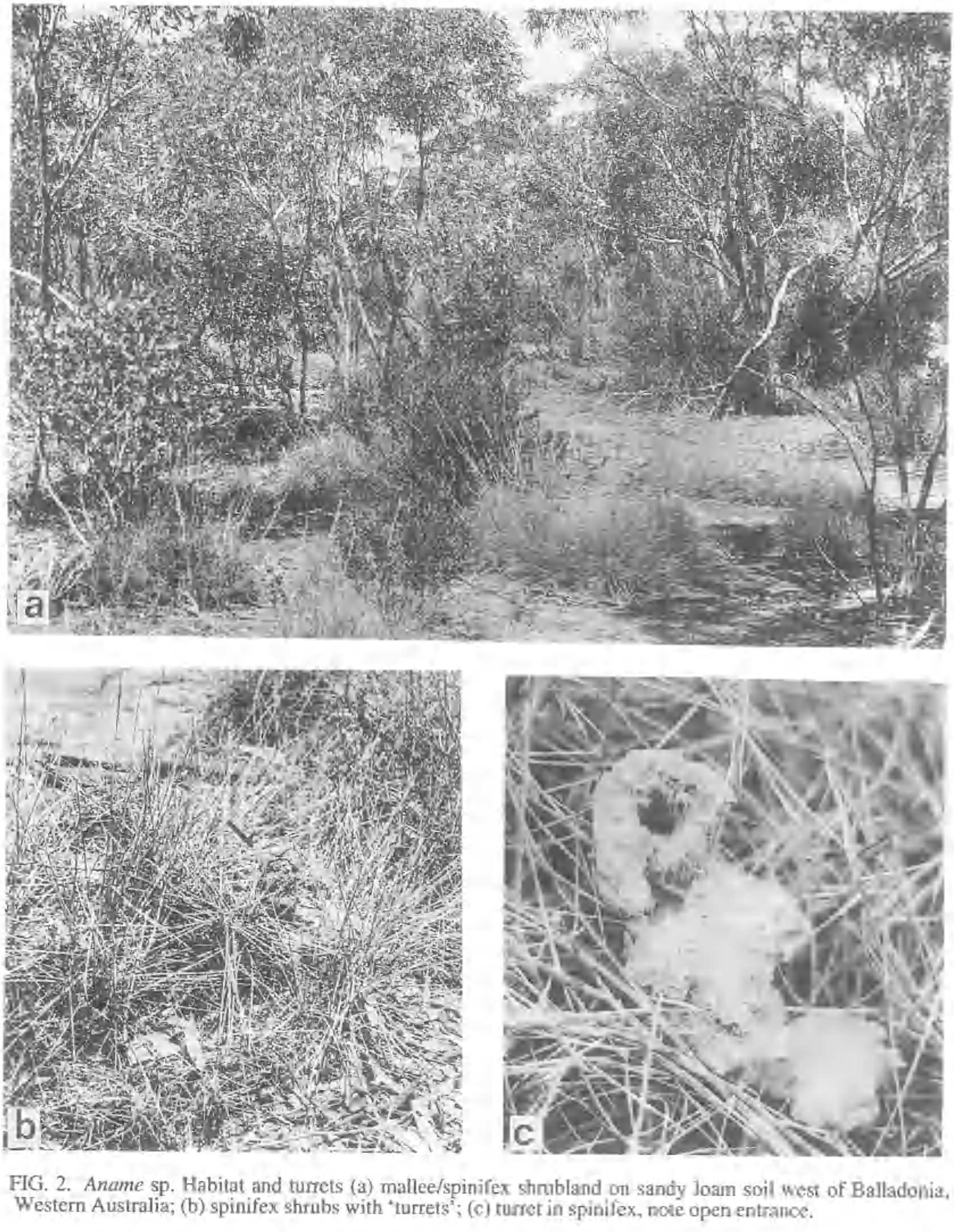

FIG. 2. *Aname* sp. Habitat and turrets (a) mallee/spinifex shrubland on sandy loam soil west of Balladonia, Western Australia; (b) spinifex shrubs with 'turrets'; (c) turret in spinifex, note open entrance.

proper) which leads into the main shaft of the burrow; a second trapdoor leads from the main shaft into a blind sideshaft (Fig. 1h). These doors provide a double safety valve in the event of flooding (Main, 1976). The false entrance/atrium functions like a pit-fall trap which 'catches' crawling insects that are then seized by the spider as it straddles the open door inside (Fig. 1h) (Main, 1982b fig. 7d). The pit-trap also provides a clear foraging area for the subterranean entrance-proper, unencumbered by the litter which would otherwise impede the plug-like door. Notable examples of elevated nests (supported against tree trunks), the primary adaptation of which has been flood avoidance but which has secondarily resulted in arboreal foraging, are those of *Misgolas robertsi* (see Mascord, 1970 p.12; Main 1976, plate B5) and *Aganippe castellum* (Main, 1986, 1987 p. 34 and fig. 6).

Spiders, the nests of which are sited on the trunks of trees but which have no contact with the ground and are thus corticolous, similarly have adopted an arboreal foraging behaviour. *Conothele* (possibly *Conothele arboricola* Pocock), *Sason* and *Chenistonia villosa* and *Moggridgea tingle* are thus all arboreal foragers although the latter two are recognised as being facultative in their behaviour. Even *Idioctis* species which extend their tubes above the tide level (or are sealed against tidal rise), sometimes against mangrove stems (Abraham, 1924), are probably in effect arboreal foragers.

However, until recently there was no known example of an Australian mygalomorph which fed in the foliage or canopy of vegetation. Therefore, the turret-building species of *Aname* is of interest. The tubes open either in gaps amongst the foliage or above the canopy of tussocks and shrubs. The spiders presumably do not venture far, if at all, away from the entrance (and are unlikely to crawl down the outside of the tube to the ground) and thus are dependent on insects creeping amongst and on the foliage and flying insects as they alight. This would mean that they are a truly foliage or canopy forager as distinct from arboreal spiders which forage on the trunks of trees and shrubs.

BURROW MODIFICATIONS AS A RESPONSE TO HISTORICAL ENVIRONMENTAL CHANGES

The arboreal tubes and most corticolous nests in mesophytic and rainforest habitats have evolved *in situ* in continuously humid habitats (but where some sites may experience extreme flooding). In contrast, of those flood-adapted nests which occur now in semi-arid and arid habitats most have evolved (*in situ*) from mesophytic denizens but as a result of a general drying of the habitat associated with climatic aridification. Paradoxically while probably making simple tubes and burrows in a "primitive", uniformly wet habitat the spiders have been exposed to the the hazard of sheet flooding as a result of periodic deluges associated with a dryer, but seasonal climate. Nevertheless, clearly a few such species do belong to taxonomic groups which already had burrows and doors well adapted to sudden deluges in rainforest and mesophytic habitats, e.g., species of *Arbanitis*.

Much of the semi-arid woodland, shrubland and saltbush steppe of southern Australia enjoyed a consistently wet climate and supported mesophytic forest and rainforest interspersed with swampland during the early Tertiary (Cookson, 1973; Cookson & Pike, 1953, 1954; Truswell, 1990). With progressive drying of the climate and development of a markedly seasonal weather pattern the vegetation was altered, leaving some relictual, moist microhabitats in juxtaposition with other seasonally alternating wet/dry microhabitats some of which now experience periodic, sudden inundation.

Certain species of trapdoor spiders whose taxonomic relatives in rainforest and mesophytic habitats lack specialised burrow structures have responded to seasonal sheet flooding in arid habitats by modifying burrow structures in flood avoidance. Notable types of burrow modification in the western part of the continent, which are hypothesised as having evolved in direct response to (geologically) historical changes in the environment are the burrows of *Aganippe castellum*, *Teyl* species with both surface and subterranean doors and the aerial tubes of the *Aname* species. Main (1986) discussed the probable origin of the semi-arboreal nest of *A. castellum*, its anti-flooding function and adoption of a 'new' foraging behaviour. This dual adaptation probably evolved during the late Miocene/Pliocene in response to fluctuating wet/dry seasons and fragmentation of the landscape into a mosaic of wet and dry microhabitats. It also has been postulated earlier (Main, 1976) that the single surface door of some *Teyl* species evolved in response to climatic/habitat changes towards a seasonal weather regime and more open habitat. The turret nest of the *Aname* species has probably, similarly developed contemporaneously, in response to the drying of the climate, in different geographic habitats but which also occur in areas subjected to some seasonal, torrential or at least very heavy rain which causes flash flooding.

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